Time in Residence Affects Escape and Agonistic Behavior in Adult Male American Lobsters

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Abstract. Acquisition and retention of a shelter by a lobster are two of the variables that play a role in lobster agonistic interactions. Since shelter procurement and retention are important for lobster survival, behaviors related to this activity frequently outrank other daily behaviors (*e.g.,* searching for food). Here, we examine the effects of time in residence on the parameters of the escape response of the American lobster, *Homarus americanus.*

Adult male intermolt lobsters (Stage C₄) were placed in an experimental tank for three different time periods (one hour, 24 hours, and 48 hours). The probability of eliciting an escape response was inversely related to the time spent in the tank. Eighty percent of the animals in residence for 1 h tailflipped in response to a threat, whereas only 14% of the animals in residence for 48 h tailflipped.

There were also significant changes in some of the parameters of the escape response among animals in residence for 24 h compared to those in residence for 1 h. The number of tailflips and the distance traveled were reduced, although frequency, velocity, acceleration, force, and work factors were not significantly different.

Furthermore, with increased time in residence, lobsters switched from an avoidance or escape-prone behavior to an aggressive-prone behavior. Most of the animals in residence for 48 h approached and attacked a threat-stimulus rather than fleeing from it. On an empirically defined "index of aggressiveness," in which various behaviors were numerically ranked from least aggressive (0) to most aggressive (6), animals residing in the tank for 1 h had an average index value of 0.1 compared to a value of 5.0 for animals in residence for 48 h.

These findings are consonant with the suggestion that lobsters that have occupied a given space for an extended period of time take possession of the site and defend it instead of fleeing when threatened with a threat-inducing stimulus; it supports the idea that shelter retention increases aggressiveness and diminishes avoidance behaviors.

Introduction

Shelter selection by American lobsters, as they make the transition from their pelagic phase to a benthic existence, has been studied in detail (Cobb and Wahle, 1994; a review). Postlarval and early juvenile lobsters actively seek out cobble and boulder habitats for shelter—a habitat that offers the most protection from predators and conspecifics as well as protection against storm surges and rapid currents (Hudon, 1987; Abe *et al.,* 1988; Incze and Wahle, 1991; Wahle and Steneck, 1991, 1992). Such shelters may be limited in number since cobble and boulder habitats comprise only 10% of the sea-floor (Kelley, 1987)—the habitat that is most favored by lobsters. In addition, as lobsters grow (up to five orders of magnitude increase in body mass), their aggressiveness increases and their behavior becomes less cryptic, so crowding may become more of a problem (Cobb and Wahle, 1994).

Shelter procurement and retention may therefore be an important determinant of overall behavior in lobsters, with dominant individuals procuring and retaining the most favorable shelters, which in turn may be important for an individual's survival (Cobb, 1971; Stewart, 1972). Recently, Spanier and others (1998) assessed the behavior of juvenile American lobsters under predation risk in labora-

tory settings. In the presence of a predator fish, the tautog, *Tautoga onitis,* the dominant lobster appeared to guard the available shelters; subdominant lobsters, which did not guard shelters, had a mortality rate seven times higher than that of dominant lobsters. Moreover, field observations by O'Neill and Cobb (1979) showed that intruders were less able to procure a shelter if the current resident had occupied it for a certain period of time.

In laboratory settings, factors that establish the dominance of an individual over other conspecifics and allow dominant individuals to have an advantage in procuring, capturing, and—more importantly—holding on to a suitable shelter include a greater carapace length and claw size (Scrivener, 1971), the sex of the individual (male), and molt stage (O'Neill and Cobb, 1979).

O'Neill and Cobb (1979) found that shelter familiarity did not affect shelter procurement or retention in the laboratory, but that in the field, lobsters already in a shelter were more likely to retain that shelter. On the other hand, American lobsters have been observed to display increased aggressiveness after being isolated in individual tanks (E. Kravitz, pers. comm. to S.C.), and during our earlier studies, we observed that it was harder to induce animals to tailflip after they had been kept for some time in isolated tanks.

Therefore, the question arises as to the extent to which an animal's time in residence is a significant determinant of its aggressive and avoidance behavior. To explore this question, we placed animals in an isolated experimental tank for periods of 1, 24, or 48 h and videotaped their responses to a nontactile threatening stimulus introduced into the tank.

We now present evidence that with increased time in residence, lobsters not only are less likely to flee from a threat, but also will confront it with increasing aggressiveness.

Materials and Methods

Procedures and experimental protocols are essentially the same as those described in Cromarty *et al.,* 1991, 1998), but are summarized here with relevant differences included.

Animals

Adult American lobsters (carapace length 78 to 84 mm) were obtained directly from an offshore lobster vessel fishing in Narragansett Bay, Rhode Island. Animals were housed at the Narragansett Bay Campus of the University of Rhode Island in separate, but connecting, tanks in a free-flow seawater system at ambient temperatures ranging from 16° to 22°C under a 14-h-light/10-h-dark illumination cycle. The animals were fed three times per week on a mixed diet of squid, crab, and fish, but were not fed for 48 h prior to an experiment. Six hours before an experiment, an animal was moved to the Kingston campus of the university, where it was placed in a holding tank (30 cm^3). The tank was supplied with its own air supply, and water was obtained from the same source used to supply the tanks at the URI Bay Campus.

Experiments

Experiments were conducted from May to October, to avoid possible seasonal differences in behavior. Lnenicka and Zhao (1991) documented seasonal differences in the physiology and morphology of crayfish neuromuscular terminals which suggested that lobster escape parameters might differ seasonally.

Experiments were carried out between 1200 and 1700 h in an aquarium filled with filtered recirculated seawater from Narragansett Bay. Salinity was measured before each experiment, and ranged between 29‰ and 33‰. Water was replaced or added as necessary to maintain salinity within this range. The experimental tank was kept between 18°C and 20°C by a Frigid Units AE-234 AG-602 chiller. The chiller was turned off before the start of the experiment. The experimental area consisted of an open-ended tank (1.0 m L × 0.3 m W × 0.3 m H) immersed in a larger main tank (2.2 m L × 0.75 m W × 0.91 m H). The layout was designed so that a threatening stimulus could be introduced at the open end of the experimental tank. A weighted wooden partition with a pulley acted as a blind—and a separation from the main tank—at the open end. To ensure that lobsters were initially at the closed, non-stimulus end, a light was placed at the open end, causing the lobster to move towards the darkened closed end. The partition was raised once the lobster had reached the closed end, while the light was moved to the *closed* non-stimulus end. This served to "push" the animal back towards the open (stimulus), now darkened, end. A piece of PVC tubing (0.15 m L × 0.10 m W) weighted to 1.45 kg with pebbles served as the threatening visual stimulus. The stimulus was raised above the open end and was released into the water at a preset distance of 10 cm (measured from the open edge of the tank to the lobster) whenever a lobster approached the open end after the designated residency period. One hour before the experiment, the physical condition of each animal was checked. Animals were used only if they moved around the tank or exhibited antennule flicking.

Cameras were placed in two positions (a Sony camcorder above the tank and a Panasonic WV-CD20 camera to the side), and experiments were recorded (Panasonic AG-6010 and Panasonic NV-8950) simultaneously from the vertical and horizontal perspectives. Video recordings of each lobster were analyzed frame-by-frame. For measurements of distance traveled, a metric grid divided into 0.5-cm units was painted onto the side of the experimental tank. Transparent overlays on the video monitor were later used to record the escape swimming distance of each animal. Distance traveled along the length of the tank was measured by

using the position of the tip of the lobster's rostrum as a guide, and the number of tailflips was counted; time was automatically recorded on the videotape. An independent observer inspected all recordings and rejected runs in which the experimental parameters were not strictly adhered to (*e.g.*, cases in which the stimulus was released closer than 10 cm to the experimental animal).

After each experiment, the animal's molt stage was determined by examining cuticular changes and setal development in the pleopods (Aiken, 1973, 1980). Only stage C_4 (intermolt) animals were used, since probability of escape depends on the molt stage of each lobster (Cromarty *et al.*, 1991, 1995). Measurements of carapace length, cutter length, lobster weight and volume, temperature, and salinity were recorded at the end of each experimental trial.

Analysis of the escape response follows our previous protocol (Cromarty *et al.*, 1991, 1998). To analyze the escape parameters, the response was broken into two elements—the initial tailflip, henceforth called the "power swim," followed by the numerous subsequent tailflips, called "subsequent swims." (The number of subsequent swims in this study ranged from one to six.) A tailflip, or swim, is defined as beginning immediately after the start of abdominal flexion and ending at abdominal extension.

The following characteristics of the escape response were analyzed for each lobster: distance traveled (centimeters), number of tailflips, duration (seconds), frequency of tailflips (tailflips per second), velocity (meters per second), acceleration (meters per second squared), force (mass × acceleration), work (force × distance), distance swum per weight (meters per kilogram), and distance swum per lobster body length. The last two parameters were measured to determine whether individual lobster variability in weight and size could alter the significance of a parameter, even though weight and size were not significantly different (using an ANOVA) among the animals in the three resident periods.

As in previous analyses, in evaluating acceleration, the added-mass forces (Batchelor, 1967) that act on accelerating bodies in fluids were ignored since these are a multiple of mass and would act equally on all animals of the same weight (see Cromarty *et al.*, 1991). The analysis of the escape response is designed to reflect relative changes in lobster escape behavior and not the kinematic relationships investigated by other researchers (Batchelor, 1967; Daniel and Meyhöfer, 1989; Nauen and Shadwick, 1993).

Each of the escape parameters was analyzed for (1) the entire escape response; (2) the initial power swim; (3) the subsequent swims over the entire subsequent swimming distance; and (4) the subsequent swims in each half of that distance, since earlier experiments showed that there were differences in the total subsequent swimming distance traveled by lobsters. We therefore divided the distance traveled in the subsequent swims by half and analyzed each half (Cromarty *et al.*, 1991, 1998). Because the distances dif-

fered and because each distance was divided equally in half for each escape sequence for each animal, no data are available to compare distance traveled between the two halves of the subsequent swims for each residency group.

To quantify the degree of "aggression" in the post-stimulus behavior of each animal, we ranked this behavior on a scale of 0 to 6 and subjectively ordered behavior towards the stimulus as follows:

0 = back away, never approach
1 = approach but remain more than one bodylength away
2 = approach within one bodylength
3 = approach, touch
4 = approach, touch, grasp
5 = approach, touch, grasp, and tug/pull
6 = approach, touch and grasp, tug/pull, and an offensive tailflip

Statistical analysis

Differences in weight, carapace length, and cutter size among the three residency periods were determined by parametric analysis of variance (ANOVA). The Fisher exact probability test (FEP) was used to determine differences in the probabilities of escape among the three resident periods.

Due to a non-normal distribution of data, Kruskal-Wallis (KW) tests were run for all the escape parameters except the subsequent swims and the "aggression intensity index." The first and second halves of the subsequent swims were compared with a multiple analysis of variance (MANOVA) and a repeated measures follow-up test. A trend was considered to exist if the P value for a parameter ranged between $0.05 < P < 0.1$. Values were considered significant at $P \leq 0.05$ for all the statistical tests. Both ANOVAs and MANOVAs were run on SPSS software ver. 6.6.1 (SPSS Inc., Chicago).

Results

Weight (in grams)/carapace length (in millimeters)/cutter length (in millimeters)

There were no significant differences in the weights (mean ± SEM for all) of 1-h (415 ± 29), 24-h (414 ± 32), and 48-h (427 ± 31) resident lobsters (ANOVA, $F(2, 27) = 0.35$, $P = 0.71$). No significant differences were found in the carapace lengths of 1-h (78 ± 4.9), 24-h (79 ± 2), and 48-h (79 ± 3) resident lobsters (ANOVA, $F(2, 27) = 0.17$, $P = 0.84$); similarly there were no significant differences in the cutter lengths of 1-h (107 ± 3), 24-h (109 ± 3), and 48-h (108 ± 2) resident lobsters (ANOVA, $F(2, 27) = 0.69$, $P = 0.61$).

Effects of residence time on the probability of escape

Probability of escape. The probability of escape for animals in the three residence time periods is summarized in

Escape and post-threat behavior of animals in each residency period; some lobsters initially tailflipped and then re-approached the stimulus or re-approached and attacked it

Residence period (h)	Immediate response		Secondary responses		
	n	Tailflip	Back up	Approach only	Approach *and* Attack
1	10	8	9	1	0
24	13	8	6	7	5
48	7	1	0	7	7

Table 1. Of the 1-h, 24-h, and 48-h resident lobsters, 8 out of 10, 8 out of 13, and 1 out of 7, respectively, escaped when the stimulus was introduced. These probabilities were significantly different (FEP, $P = 0.001$).

Escape parameters for one- and 24-hour resident male adult lobsters. Because only one lobster among the 48-h resident group could be induced to tailflip, only 1-h and 24-h residents were compared. Three lobsters in the 1-h resident period were not analyzed, because their gross swimming pattern deviated from a rectilinear motion; thus five 1-h lobsters and eight 24-h lobsters were used in the analyses.

Total escape response (initial power swim plus subsequent swims). One-hour resident lobsters swam farther (KW, $\chi^2 = 6.19$, $P = 0.012$) and took more tailflips (KW, $\chi^2 = 5.67$, $P = 0.017$) than did 24-hour resident animals (Fig. 1A, B, respectively). Distance-dependent parameters, such as distance traveled per body length and distance traveled per weight, were significantly shorter among the 24-h lobsters (KW, $P = 0.02$; Fig. 1C, D). Although time spent escaping, frequency of tailflips, velocity, acceleration, force, and work were not significantly different at the $P \leq 0.05$ level between the two groups (KW, $P > 0.05$), a trend at $0.05 < P < 0.10$ towards a decrease in time, frequency, and velocity was observed for the 24-h resident lobsters (Fig. 2A, B, and C).

Initial power swim. There was a significant decrease in the acceleration, force, and work of the power stroke in lobsters that were in residence for 24 h (KW, $P \leq 0.05$; Fig. 3A, B, and C) and a significant increase in the duration of the initial power stroke (KW, $P = 0.014$; Fig. 3D). A trend towards decreased distance traveled and lower velocity in the 24-h resident lobsters was observed (KW, $0.05 < P < 0.10$).

Total subsequent swims. Five males in the 1-h category and six males in the 24-h category were compared, since two lobsters in the 24-h resident period took only one tailflip with no subsequent swims. Significant differences in subsequent swim duration were found between animals in the 1-h to 24-h resident periods. Significant differences in subsequent swim duration (MANOVA, $F(1, 9) = 3.92$, $P =$

0.04), and number of tailflips (MANOVA, $F(1, 9) = 7.42$, $P = 0.02$) were found, with 24-h resident lobsters spending less time tailflipping and taking fewer tailflips (Fig. 4A, B).

Post-threat behavior

In the analysis of post-threat behaviors, the percentage of lobsters that re-approached the stimulus was 0% (0 out of 10), 54% (7 out of 13), and 100% (7 out of 7), in the residency periods of 1 h, 24 h, and 48 h, respectively (Table I). Of these, 0% (0 of 10) of the 1-h, 38% (5 of 13) of the 24-h, and 100% (7 of 7) of the 48-h lobsters approached *and* attacked the stimulus with high intensity after it had been
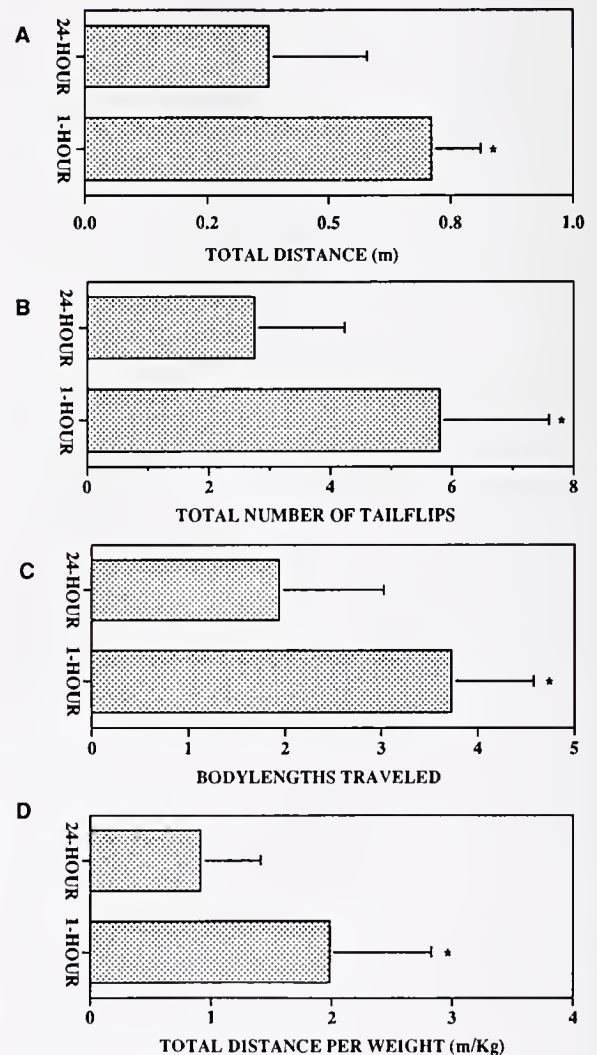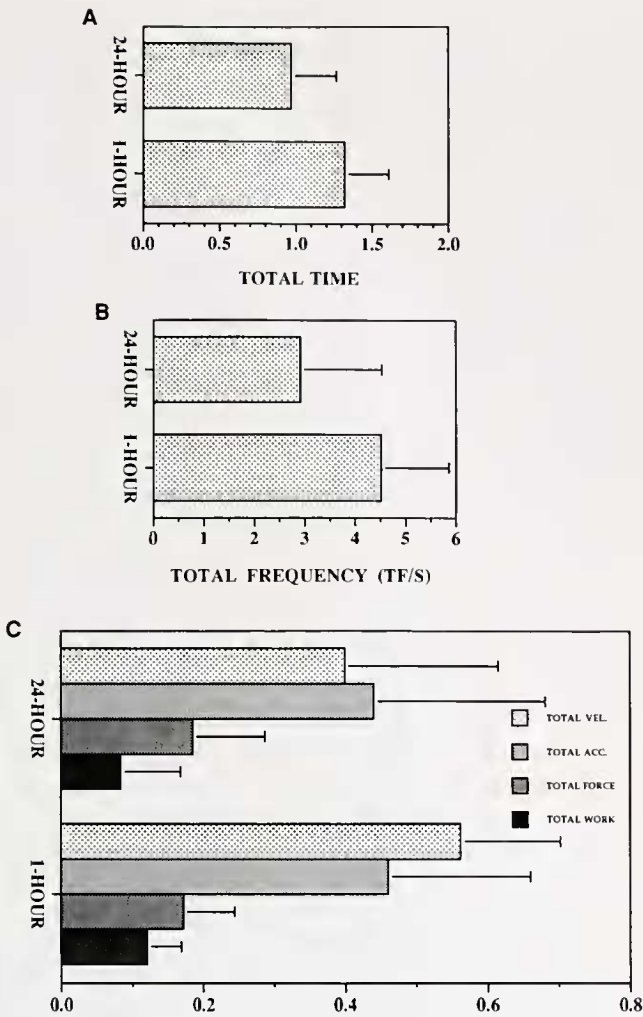

Figure 1. Parameters of the entire escape response exhibited by lobsters in residence for 1 h ($n = 5$) and 24 h ($n = 8$). An asterisk (*) indicates results that are significantly different at $P \leq 0.05$. (A) Mean distance traveled in meters (m). (B) Mean number of tailflips. (C) Mean distance traveled divided by lobster body length; represented as number of body lengths traveled. (D) Mean distance traveled in meters (m) divided by lobster weight in kilograms (kg).

Figure 2. Parameters of the entire escape response exhibited by lobsters in residence for 1 h ($n = 5$) and 24 h ($n = 8$). (A) Mean time in seconds (s). (B) Mean frequency of tailflips in tailflips per second (TF s^{-1}). (C) Mean velocity in meters per second (m s^{-1}), acceleration in meters per second squared (m s^{-2}), force in newtons (kg m s^{-2}), and work in joules (J) of tailflips.

distinct change in behavior compared to the 24-h resident animal, exhibiting more grasping, pulling, and offensive tailflips. After the experiment, all animals (while still in the experimental tank) ate the food presented to them, indicating that they were not under stress, since sick or stressed animals avoid food altogether (pers. obs.).

Discussion

In this study, we have shown that lobsters residing in an experimental tank for 24 or 48 hours exhibit a reduced tendency to escape in response to a threat and an increase in post-threat aggressiveness.

Figure 3. Parameters of the power stroke exhibited by lobsters in residence for 1 h ($n = 5$) and 24 h ($n = 8$). An asterisk (*) indicates results that are significantly different at $P \leq 0.05$. (A) Mean acceleration in meters per second squared (m s^{-2}). (B) Mean force in newtons (kg m s^{-2}). (C) Mean work in joules (J). (D) Mean duration in seconds (s).
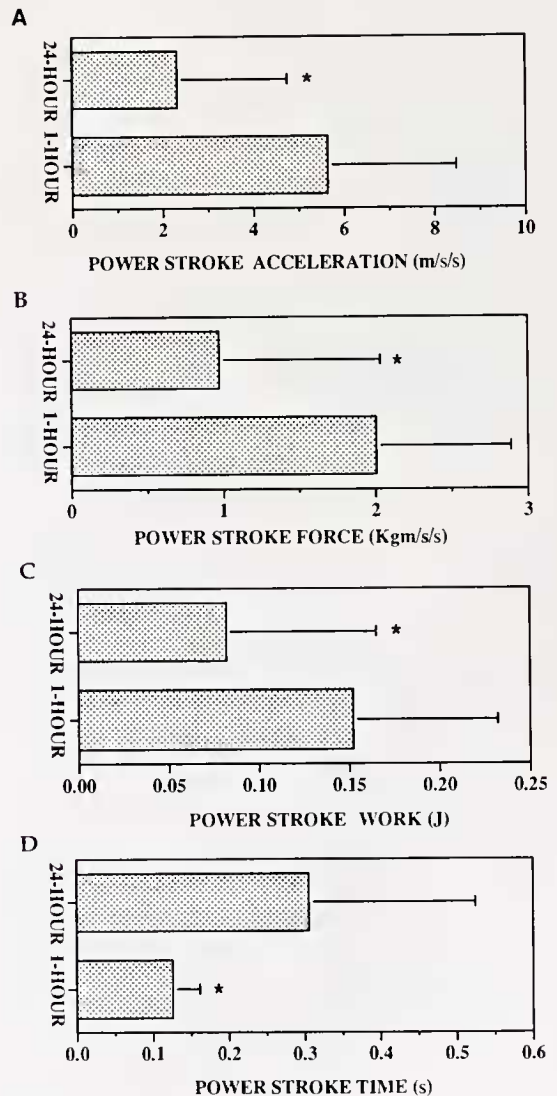
presented. On the aggression intensity index, (with predetermined levels of aggressive behavior, ranked from 0 to 6, see Methods), behavioral responses after the stimulus was introduced were statistically different (Fig. 5A–C), with lobsters in residence for 48 h displaying more intensively aggressive behaviors (average index of 5.0 ± 0.8) than those in residence for 24 h (average index of 2.1 ± 2.2; KW, $P = 0.03$) and 1 h (average index of 0.1 ± 0.3; $P = 0.006$).

Although it is possible that stress influenced these behaviors, no physical evidence of stress-related behavior was observed. Animals in all three residency periods exhibited typical active searching and antenna whipping behavior. (Lobsters that exhibit stress show no movement in the experimental tank and do not antenna whip [pers. obs.].) In addition, lobsters in the 48-h residency period showed a
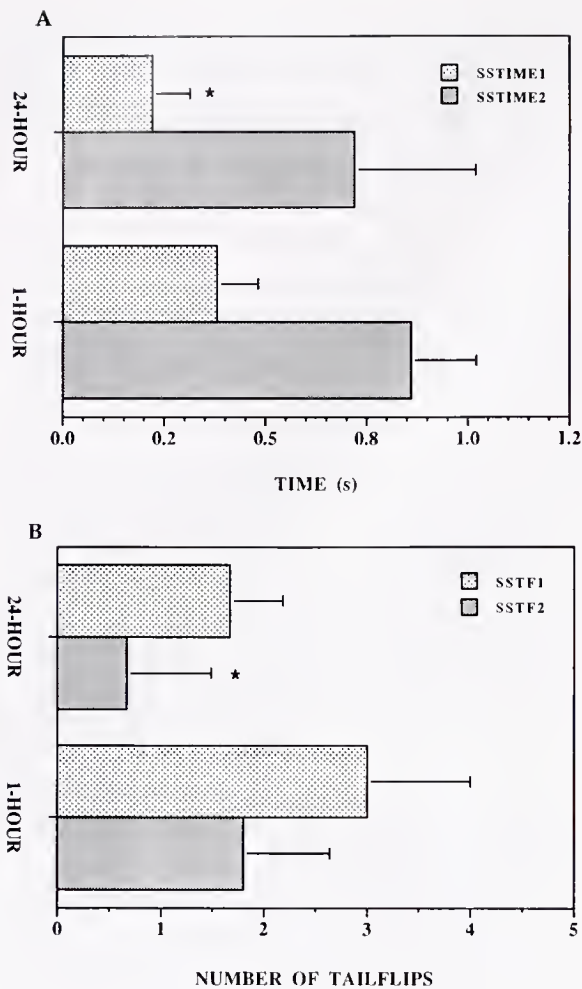
Figure 4. Parameters of subsequent swims of the escape response exhibited by lobsters in residence for 1 h (*n* = 5) and 24 h (*n* = 8). An asterisk (*) indicates results that are significantly different at $P \leq 0.05$. (A) Mean duration in seconds (s) for the first (SSTtME1) and second (SSTtME2) halves of the subsequent swimming distance. (B) Mean number of subsequent swims in the first (SSTF1) and second (SSTF2) halves of the subsequent swimming distance.

The measured parameters of the escape response (distance traveled, number of tailflips, acceleration, force, etc.) were all reduced in the 24-h residency group, while time spent escaping was increased. The efficacy of the initial power stroke was reduced, resulting in animals that appeared reluctant to escape. The power swim took longer to complete and the distance traveled was reduced, resulting in a lower initial velocity and acceleration (Figs. 1 and 2). Lobsters residing in the tank for 48 h simply did not tailflip, and therefore their escape response sequences could not be compared to those of 1-h and 24-h residency animals.

The post-stimulus behavior of the 24-h and 48-h resident lobsters was different from that of the 1-h residents. None of the latter attacked the stimulus, but 38% of the 24-h and 100% of the 48-h lobsters attacked the stimulus with high intensity, as reflected in the aggression intensity index. In particular, the 48-h resident lobsters exhibited the highest intensity of aggressive behaviors towards the stimulus (Fig. 5C). Therefore, as residency period was increased from 1 h to 48 h (in an experimental tank), escape behavior decreased and directed aggression towards the stimulus increased.

Our experiments were designed to test whether time in residence affects the probability that a lobster will respond with an escape response when threatened. Since animals tailflipped when initially caught and again when placed in the experimental tank, we tried to minimize handling by capturing them with a net (in their holding tanks) and then moving them directly to the experimental tank. To avoid handling-induced arousal, we did not re-handle 24-h and 48-h lobsters once they were placed in the experimental tank. In preliminary experiments we found that any attempt to recapture an animal caused it to tailflip wildly around the tank. In any event, although the interval between handling and presentation of a threat may have been different in the three groups, it is unlikely that a single prior handling would
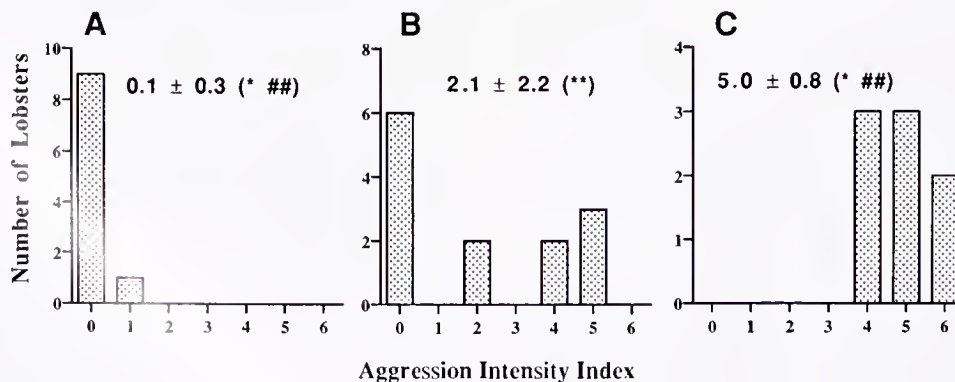
Figure 5. Average aggression intensity index of post-threat behaviors directed towards the stimulus by lobsters in residence for 1 h (A), 24 h (B), and 48 h (C). Index values range from 0 (back away, never approach) to 6 (grasp, pull, tug, and aggressive tailflip). The asterisks and number symbols indicate the level of significance: * 1 h < 24 h; P = 0.03; ## 1 h < 48 h; P = 0.0006; ** 24 h < 48 h; P = 0.009.

produce significant differences in the level of arousal in 24-h and 48-h residents.

Nonetheless, if prior handling contributed to the observed time-dependent reluctance to escape and increase in aggressiveness, then our findings suggest that an animal becomes more aggressive the longer it is left undisturbed in a site.

Many other factors appear to affect an animal's ability to procure and retain a shelter (O'Neill and Cobb, 1979). These include differences in dominance due to body length, weight, and claw size (Scrivener, 1971). Reproductive status is also important. In a related decapod, maternal female crayfish residents won 92% of their encounters with male intruders (Figler et al., 1995). Gravid lobsters exhibit a distinct reduction in escape behavior and are more likely than males to attack an approaching stimulus (Cromarty et al., 1998). Odor cues for discrimination of familiar and dominant lobsters (Karavanich and Atema, 1991, 1993, 1998a, b) and sex-identifying urine and molt signals in lobsters (Atema and Cowan, 1986), plus visual cues (Bruski and Dunham, 1987), are most likely important sensory cues for procuring and residing in a shelter. Crayfish rapidly learn to discriminate between changing spatial configurations (Sandeman and Varju, 1988; Varju and Sandeman, 1989; Basil and Sandeman, 1997) and, as shown by direct measurements of electrical heart activity (Shuranova and Burmistrov, 1995), are constantly sampling their surroundings (i.e., predators or conspecific intruders, currents, shadows, food availability, etc.).

An important determinant in shelter retention may be social contact with conspecifics. Hoffman et al. (1975) showed that lobsters who were in visual contact with other animals or were communally housed were less aggressive. In this regard, Yeh et al. (1996, 1997) found that crayfish social status and social experience determine the effect of serotonergic modulation on the lateral giant motor neuron that mediates one form of escape behavior. Social isolation has also been found to cause dramatic increases in intraspecific aggression in mice (Valzelli, 1973).

In an early study, O'Neill and Cobb (1979) found that in the laboratory, shelter familiarity did not affect shelter procurement or retention, whereas in the field, resident lobsters were more likely to retain their shelters. These observed differences might have been due to the above-mentioned experimental conditions, i.e., type and duration of the experimental housing of animals.

In our experimental conditions there were no other animals, no places to seek shelter, and only one avenue of escape. Therefore, an animal's immediate response under these circumstances may be considered to reflect and be driven by the differential effects of having been undisturbed in a familiar environment for different lengths of time. That is, our experiments seem to reveal that the patterns associated with either aggression and dominance, on the one hand, or avoidance and submission, on the other, become mani-

fested as a function of how the animal assesses its own place in its immediate environment. This assessment then becomes a determinant of how an animal responds to other conspecifics and might be considered operationally as a "motivational state." A change in "motivational state" has recently been tested in the European hermit crab *Pagurus bernhardus* during agonistic encounters (Elwood et al., 1998). This study showed that the duration and severity of the startle/threat response are inversely related to the "motivational state" of the animal to continue the previous activity, namely of fighting for a more suitable shelter inhabited by a conspecific.

In summary, our experiments indicate that time in residence and isolation are important physiological determinants of a lobster's behavior and can cause it to switch from an avoidance-prone to an aggression-prone state.

Acknowledgments

Literature Cited

Able, K. W., K. L. Heck, M. P. Fahay, and C. T. Roman. 1988. Use of salt-marsh peat reefs by small juvenile lobsters on Cape Cod, Massachusetts. *Estuaries* **11:**83–86.

Aiken, D. E. 1973. Proecdysis, setal development, and molt prediction in the American lobster (*Homarus americanus*). *J. Fish. Res. Board Can.* **30:**1334–1337.

Aiken, D. E. 1980. Molting and growth. Pp. 91–163 in *The Biology and Management of Lobsters.* vol. 1, J. S. Cobb and B. F. Phillips, eds. Academic Press, New York.

Atema, J., and D. Cowan. 1986. Sex-identifying urine and molt signals in lobster (*Homarus americanus*). *J. Chem. Ecol.* **12:**2065–2080.

Basil, J., and D. Sandeman. 1997. Australian freshwater crayfish detect small spatial changes in their habitat using only tactile cues. *Soc. Neurosc. Abstr.* **23:**527.17.

Batchelor, G. K. 1967. *An Introduction to Fluid Dynamics.* Cambridge University Press, London.

Bruski, C. A., and D. W. Dunham. 1987. The importance of vision in agonistic communication of the crayfish *Orconectes rusticus*. I. An analysis of bout dynamics. *Behaviour* **63:**83–107.

Cobb, J. S. 1971. The shelter behavior of the American lobster, *Homarus americanus*. *Ecology* **52:**108–115.

Cobb, J. S., and R. A. Wahle. 1994.   Early life history and recruitment processes of clawed lobsters. *Crustaceana* **67**:1–25.

Cromarty, S. I., J. S. Cobb, and G. Kass-Simon. 1991.   Behavioral analysis of the escape response in juvenile American lobsters, *Homarus americanus* over the molt cycle. *J. Exp. Biol.* **158**:565–581.

Cromarty, S. I., J. S. Cobb, and G. Kass-Simon. 1995.   Adult and juvenile lobsters (*Homarus americanus*), differ markedly in the neuromuscular physiology and behavior of the escape response over the molt cycle. *Soc. Neurosci. Abstr.* **25**:201.

Cromarty, S. I., J. Mello, and G. Kass-Simon. 1998.   Behavioral analysis of escape behavior in male, and gravid and non-gravid, female lobsters. *Biol. Bull.* **194**:63–71.

Daniel, T. L., and E. Meyhöfer. 1989.   Size limits in escape locomotion of caridean shrimp. *J. Exp. Biol.* **143**:245–265.

Elwood, R. W., K. E. Wood, M. B. Gallagher, and J. T. A. Dick. 1998.   Probing motivational state during agonistic encounters in animals. *Nature* **393**:66–68.

Figler, M. H., M. Twum, J. E. Finkelstein, and H. V. S. Peeke. 1995.   Maternal aggression in red swamp crayfish (*Procambarus clarkii,* Girard): The relation between reproductive status and outcome of aggressive encounters with male and female conspecifics. *Behaviour* **132**:107–125.

Hoffman, R. S., P. J. Dunham, and P. V. Kelly. 1975.   Effect of water temperature and housing conditions upon the aggressive behavior of the lobster *Homarus americanus. J. Fish. Res. Board Can.* **32**:713–717.

Hudon, C. 1987.   Ecology and growth of postlarval and juvenile lobster *Homarus americanus,* off îles de la Madeleine (Quebec). *Can. J. Fish. Aquat. Sci.* **50**:1422–1434.

Incze, L., and R. A. Wahle. 1991.   Recruitment from pelagic to early benthic phase in lobsters (*Homarus americanus*). *Mar. Ecol. Progr. Ser.* **79**:77–87.

Karavanich, C., and J. Atema. 1991.   Role of olfaction in recognition of dominance in the American lobster (*Homarus americanus*). *Biol. Bull.* **181**:359–360.

Karavanich, C., and J. Atema. 1993.   Agonistic encounters in the American lobster, *Homarus americanus:* Do they remember their opponents? *Biol. Bull.* **185**:321–322.

Karavanich, C., and J. Atema. 1998a.   Olfactory recognition of urine signals in dominance fights between male lobsters. *Behavior* **135**:719–730.

Karavanich, C., and J. Atema. 1998b.   Individual recognition and memory in lobster dominance. *Anim. Behav.* **56**. (in press).

Kelley, J. 1987.   A treatise on glaciated coast. Pp. 151–176 in *Sedimen-tary Environments Along Maine's Estuarine Coastline,* D. M. Fitzgerald and P. S. Rosen, eds. Academic Press, New York.

Lnenicka, G. A., and Y. Zhao. 1991.   Seasonal differences in the physiology and morphology of crayfish motor terminals. *J. Neurobiol.* **22**:561–569.

Nauen, J. C., and R. E. Shadwick. 1993.   Biomechanics of tail-flipping by the spiny lobster *Panulirus interruptus. Am. Zool.* **32(5)**:127A.

O'Neill, D. J., and J. S. Cobb. 1979.   Some factors influencing the outcome of shelter competition in lobsters (*Homarus americanus*). *Mar. Behav. Physiol.* **6**:33–45.

Sandeman, D., and D. Varju. 1988.   A behavioral study of tactile localisation in the crayfish *Cherax destructor. J. Comp. Physiol.* **163**:525–536.

Scrivener, J. C. E. 1971.   Agonistic behavior of the American lobster, *Homarus americanus* (Milne-Edwards). *Fish. Res. Bd. Can. Tech. Rep.* **235**:1–128.

Shuranova, Z. H., and I. U. Burmistrov. 1995.   The orienting reaction in invertebrates. *Zh. Vyssh. Nerv. Deat. Im. IP. Pavola.* **45(3)**:510–520.

Spanier, E., T. P. McKenzie, J. S. Cobb, and M. Clancy. 1998.   Behavior of juvenile American lobsters, *Homarus americanus,* under predation risk. *Mar. Biol.* **130**:397–406.

Stewart, L. L. 1972.   The seasonal movements, population dynamics and ecology of the lobster, *Homarus americanus* (Milne Edwards) off Ram Island, Connecticut, Ph.D. Thesis, University of Connecticut, 152 pp.

Valzelli, L. 1973.   The "isolation syndrome" in mice. *Psychopharmacologia* **31**:305–320.

Varju, D., and D. Sandeman. 1989.   Tactile learning in a new habitat and spatial memory in the crayfish *Cherax destructor.* Page 21a in *Dynamics and Plasticity in Neuronal Systems.* N. Elsner and W. Singer, eds. Thieme, Stuttgart.

Wahle, R. A., and R. S. Steneck. 1991.   Recruitment habitats and nursery grounds of the American lobster *Homarus americanus:* a demographic bottleneck. *Mar. Ecol. Progr. Ser.* **69**:231–243.

Wahle, R. A., and R. S. Steneck. 1992.   Habitat restrictions in early benthic life: experiments on habitat selection and *in situ* predation with the American lobster. *J. Exp. Mar. Biol. Ecol.* **157**:91–114.

Yeh, S. R., R. A. Fricke, and D. H. Edwards. 1996.   The effect of social experience on serotonergic modulation of the escape circuit of crayfish. *Science* **271**:366–369.

Yeh, S. R., B. E. Musolf, and D. H. Edwards. 1997.   Neuronal adaptations to changes in the social dominance status of crayfish. *J. Neurosci.* **17**:697–708.